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RESEARCH ARTICLE

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Spatial distribution of Annonaceae across biomes and anthromes: Knowledge gaps in spatial and ecological data

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Societal Impact Statement
The United Nations Decade on Ecosystem Restoration underlines the importance of understanding how different taxa are affected by human induced, global changes in ecosystems. Here, we investigate if this impact can be quantified for the globally distributed tropical plant group Annonaceae (Soursop family) using distributional data and International Union for Conservation of Nature (IUCN) Red List assessments. We find that even for a taxonomically well-studied tropical plant family such as Annonaceae, little is known about the true distribution and ecological requirements of, and threats to, species in this group. We discuss several improvements in data collection that should enable more in-depth analyses in the future.

Summary

- The Sustainable Development Goals of the United Nations (UN), formulated with the overarching aims to end poverty and protect the planet, are also aimed at implementing sustainable management of all types of forests, to stop deforestation and to restore degraded forests. This led to the declaration of the UN Decade on Ecosystem Restoration. To meaningfully restore ecosystems, it is important to increase our understanding on the distribution of taxa and obtain insight in how different taxa are affected by human induced, global changes in ecosystems.
- Here, we investigate if this impact can be quantified for the globally distributed tropical plant group Annonaceae (Soursop family) using spatial data and International Union for Conservation of Nature (IUCN) Red List assessments. Insight is gained in how Annonaceae are distributed over biomes and anthropogenic biomes (anthromes) and how threatened Annonaceae are based on their distribution.
- We find that even for a taxonomically well-studied group such as Annonaceae, very little is known about the true distribution and ecological requirements of, and threats, to species.
- We urge to invest in (1) the exploration of ecological requirements of species in relation to their genetic patterns, in order to understand the impact of ecosystems

changes, (2) research on distributional patterns in a temporal framework as the available data collected over decades might not reflect current distributions over biomes and anthromes well and (3) high-quality spatial data collection that should adhere to the Findability, Accessibility, Interoperability and Reuse (FAIR) data principles, so that the quality of spatial analyses as well as IUCN Red List assessments will increase.

KEYWORDS

Anthropocene, conservation, geographic information system (GIS), herbarium collections, higher-taxon approach, plant distributions

1 | INTRODUCTION

In 2015, 17 Sustainable Development Goals (SDGs) were formulated by the United Nations with the aims to end poverty, protect the planet and ensure that people worldwide can enjoy peace and prosperity (UN General Assembly, 2015). SDG 15 aims to 'protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss'. More specifically, subgoal 15.2 states that the implementation of sustainable management of all types of forests should be promoted, deforestation halted, degraded forests restored and afforestation and reforestation substantially increased globally (UN General Assembly, 2015). This attention is needed because forests cover approximately 42 million km^2 in tropical, temperate and boreal lands (this is approximately 30% of the total land surface; Bonan, 2008). Besides their surface, they provide important ecosystem services, such as food, timber and fuel production; water regulation at global and local scales (including conservation, prevention of floods and droughts, and watershed protection); nutrient retention; carbon sequestration; biodiversity protection; climate change mitigation and climate regulation (including reduced risk of natural disasters, including landslides and other extreme events and contribution to the balance of oxygen, carbon dioxide and humidity in the air); ecotourism; and spiritual and traditional values (Aznar-Sánchez et al., 2018; Bonan, 2008; UN General Assembly, 2015). Notwithstanding all these functions and services, much less is known about forest biodiversity–ecosystem functioning compared to better-studied systems such as grasslands (Mori et al., 2017). For instance, some report that forests have a higher structural complexity, contain dominant taxa with longer life cycles and have larger-scale spatiotemporal dynamics (Scherer-Lorenzen, 2014), whereas others found that disturbances interrupt these longer life cycles to make the vegetation to more dynamic (Reis et al., 2022). Fast demographic traits (i.e., short turnover times) can lead to high diversification rates (Baker et al., 2014) although also long-term persistence of species has been reported based on high ecological stability (Pennington et al., 2010; Pennington & Lavin, 2016). Given the enormous biodiversity in tropical forests and the high complexity of their ecosystems, studying their dynamics is very complicated.

Covering approximately 7% of the terrestrial portion of the earth's surface (Hill & Hill, 2001), tropical rain forests harbour approximately 45% of all terrestrial species (Eiserhardt et al., 2017), which includes approximately three fourth of all tree species (Singh & Sharma, 2009). This is equivalent to an estimated 40,000–53,000 tropical tree species (Rivers et al., 2022; Slik et al., 2015) out of a total between 60,000–73,000 estimated worldwide (Beech et al., 2017; Botanic Gardens Conservation International, 2021; Cazzolla Gatti et al., 2022). The tropical rain forest is distributed across sub-Saharan Africa, Madagascar, South-East Asia, northern Australia, a large portion of the islands of the Pacific Ring of Fire and Central and South America (Eiserhardt et al., 2017; Morley, 2000). Although humans have impacted tropical forests long before modern times (van der Sande et al., 2019; van Gemerden et al., 2003), they are currently at risk because of increasing anthropogenic activities (Antonelli, 2021; Wiens, 2016). Especially during the last few decades, humans increasingly influenced the earth's surface to meet their needs (Gibbs et al., 2010). As a result, most natural biomes have changed into anthropogenic biomes, also called Anthromes (Ellis et al., 2010). The resulting land use changes impacted ecosystems in many ways (FAO & UNEP 2020), for instance via a loss of biodiversity (Hobbs et al., 2006) or the alteration of soil quality (Chen, 2007). Another consequence of increased anthropogenic activities is increased air pollution, causing an alteration of climatic patterns via enhancement of the greenhouse effect (Ramanathan & Feng, 2009) and radiative forcing (Collins et al., 2006). Because all species have distinct ranges of conditions that determine where they can occur (Wiens, 2016), the impact of these changes for species (including humans) cannot be denied (Pecl et al., 2017; Román-Palacios & Wiens, 2020), although the exact traits that determine species ranges are still not clear (Freeman et al., 2018; MacLean & Beissinger, 2017). Understanding how different taxa are affected by these changes is key in order to inform measures for conservation and protection (Rivers et al., 2022), something especially important in this UN Decade on Ecosystem Restoration. Given that approximately 60% of all vascular plant species occur in tropical forests (Burley, 2002; FAO & UNEP, 2020), understanding the impact of ecosystem changes in this biome is crucial. Unfortunately, up to now, we have little insight in this.

In this study, we make a first attempt to use the available spatial data on the pantropical and rain-forest restricted (Punyasena et al., 2008) plant family Annonaceae (the Soursop family) to gain insight in how this taxon is distributed over natural biomes and anthropogenic biomes (anthromes). We combine these spatial data with published and drafted IUCN Red List assessments that were assessed in the context of the Global Tree Assessment project (Beech et al., 2017; Botanic Gardens Conservation International, 2021), to investigate how Annonaceae are distributed over a human-impacted globe. Because the analyses done here were not free from problems, we share our experiences in order to improve such attempts in the future and in this way contribute to a better assessment of the impact of humans on the tropics.

2 | MATERIALS AND METHODS

2.1 | Study system

The plant family Annonaceae occurs in tropical to subtropical regions around the world (with a single temperate genus in the eastern U.S.A. (*Asimina*). It is by far the most diverse family in the clade Magnoliales at the genus as well as the species level. It currently holds 110 genera and over 2500 species of trees, shrubs and lianas (Chatrou, Pirie, et al., 2012; Chatrou et al., 2018; Guo et al., 2017; Couvreur unpublished data). The four subfamilies (Anaxagoreoideae [approximately 30 spp.], Ambavioideae [approximately 60 spp.], Annonoideae [approximately 1600 spp.] and Malmeoideae [approximately 800 spp.]) all contain members from different continents and are regarded as important ecological components of lowland tropical forest ecosystems (Chatrou, Erkens, et al., 2012; Couvreur, Pirie, et al., 2011; Richardson et al., 2004). It has been shown that their abundance and richness increases with higher temperature and precipitation (Punyasena et al., 2008).

Morphologically, the family can be recognised by a combination of traits such as an aromatic, fibrous bark; alternate, distichous and entire leaves without stipules; a whorled floral phyllotaxis, plicate carpels and trimerous perianth (Saunders, 2010). Fruits are generally a cluster of one-to-many free or fused monocarps. Lastly, the broad and high multiseriate xylem rays are a wood anatomical character characterising Annonaceae (Koek-Noorman & Westra, 2012).

2.2 | Taxonomic data sources

Because Annonaceae are taxonomically well studied (see for instance for the Neotropics: Erkens et al., 2017; for Africa: Hoekstra et al., 2021; and for Asia: Meade & Parnell, 2018), many herbarium specimens have become available over the years. A well worked-out taxonomy is important for making inferences within a family, because without it, analysis can result in faulty conclusions, mismatched records and inflated species numbers (Boyle et al., 2013). Data were therefore primarily collected from recent monographs and revisions, from examining herbarium specimens during ongoing herbarium work for flora projects (e.g., Flora Neotropica, Flora of the Guianas, Flora do Brazil and Flora de Gabon) and from the databases BIEN (for the Neotropics; https://bien.nceas.ucsb.edu/bien/; Maitner et al., 2018) and RAINBIO (for Africa; https://gdauby.github.io/rainbio/index.html; Dauby et al., 2016). GBIF data (Global Biodiversity Information Facility [GBIF]; https://www.gbif.org/) were only used in instances when insufficient specimen data were available based on the previous data sources. GBIF data were restricted to accessions with a coordinate uncertainty of less than 1000 m. The resulting data set consisted of 108 out of 110 Annonaceae genera (Table S1) and 67,966 specimens.

Because the highest likelihood of taxonomic mistakes lies at the species level, all analyses were carried out at the genus level, a so-called higher-taxon approach (Gaston & Williams, 1993). This allowed us to aggregate occurrence data of a large number of species (and specimens) at large spatial scales and should result in less error due to missing or unreliable identifications at the species level (ter Steege et al., 2006). Furthermore, noise through sampling bias as well as collector and locality bias in a species-level analysis (Haripersaud, 2009; Küper et al., 2006; ter Steege et al., 2011) is overcome at the genus level due to the bigger sample size. Hence, a higher-taxon approach can aid in generating information on large-scale biogeographic distribution patterns (Dagallier et al., 2020; Gaston et al., 1995). We assume that genus identifications are more correct, because generic limits are fairly clear for most genera in Annonaceae. We feel that our current data set does not allow for an in depth, species-level analysis of Annonaceae.

2.3 | Biome types and biomes

In this work, we analyse Annonaceae distribution at the level of biomes. Although the term biome is used in a multitude of ways, many ecological and biogeographical studies have used this concept to characterise the world's environment (see Mucina, 2019 for a review of the concept). Given their macro-level nature, they cannot be used for fine-scale analyses (Pennington et al., 2004), as opposed to ecoregions or sub-biomes (Virtanen et al., 2016), which take into account community interactions (Olson et al., 2001) and fine-scale environmental factors (Mucina, 2019). Given our higher-taxon approach (see above) and the data set at hand, we feel that this concept is at the right level to probe global spatial patterns in Annonaceae. We did not apply the concept of ecoregions here because we did not want to concentrate on a single geographical area. This would remove us from our global approach (Pennington et al., 2004). Furthermore, ecoregions are much smaller than biomes, and consequentially, there are many more of them. For instance, Olson et al. (2001) delimited 867 ecoregions. This level of detail would not provide any useful insights with our data set.

In addition to the biomes described by Olson et al. (2001), the analysis has also been done with more generic terrestrial biome types (clusters of similar biomes), comparable with the Zonobiomes of Walter and Box (1976), also used by for instance Schrire et al. (2005).

Because our study focusses on woody trees and lianas, we have defined our general biome types as (1) desert, (2) grassland, (3) taiga, (4) temperate vegetation with trees (forests, savannas and shrublands), (5) tropical vegetation with trees (forests, savannas and shrubland) and (6) tundra (Figure 1). Clusters 4 and 5 are used to emphasise the disjunction between tropical and non-tropical biome types, because Annonaceae have always been positioned as a tropical group (with the exception of *Asimina*).

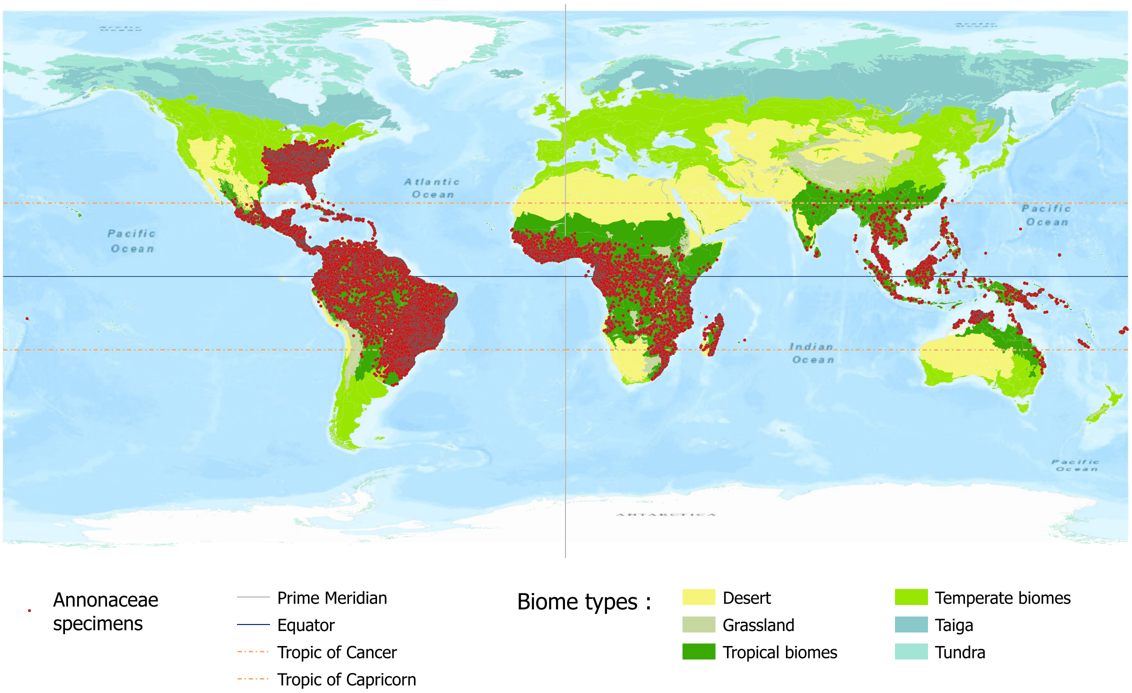

FIGURE 1 Global distribution of Annonaceae based on 67,966 specimens after cleaning over six biome types: desert, grassland, temperate vegetation with trees (forests, savannas and shrublands), tropical vegetation with trees (forests, savannas and shrublands), taiga and tundra. A single dot indicates a geolocated Annonaceae specimen.

TABLE 1 Feature data layers used for the analyses of Annonaceae distribution across biomes and anthromes

Feature	Name and type of the layer	Owner—credits/sources	Date modified
Basemap	World topographic map	Source: Esri, HERE, Garmin, Intermap, increment P Corp., BEGCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), © OpenStreetMap contributors, and the GIS User Community	/
Basemap	World Imagery with labels	Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community	/
Anthromes	Anthropogenic biomes of the world—2000 (data basin data set)—raster	Consbio—Ellis et al. (2010)	09/09/2010
Biomes	Biomes and ecoregions 2017—polygon	Esri_landscape2—Bioscience, An Ecoregions-Based Approach to Protecting Half the Terrestrial Realm https://doi.org/10.1093/biosci/bix014	24/06/2021
Continents	World continents—polygon	Esri_dm—ESRI	19/05/2020
Countries	World countries (generalised)—polygon	Esri_dm—Sources: Esri; Garmin International, Inc.; U.S. Central Intelligence Agency; National Geographic Society	12/10/2021
Important longitude and latitude lines	World GeoReference Lines—simple feature	Esri_dm—ESRI	13/10/2021

TABLE 2 Number of Annonaceae genera, species and specimens per continent based on our data set

Continent	Number of genera	Number of species	Number of specimens	Percentage of specimens
Africa	44	404	18,375	27.0%
Asia	41	422	2923	4.3%
Australia	14	31	1821	2.7%
North America	2	10	3257	4.8%
Oceania	13	36	124	0.2%
South and Central America	33	578	41,466	61%

2.4 | Spatial analyses

The specimen data were plotted using ArcGIS Pro version 2.9.1 (Environmental Systems Research Institute, 2021), showing continents, country borders, biome types, biomes and anthromes (for feature data layers, see Table 1). Plotted points that did not match the known generic ranges (as described in taxonomic papers and as represented on the Kew Plants of the World website; https://powo.science.kew.org/) or occurred in water were removed when these misplacements were not due to correctable georeferencing mistakes. When it was unclear how misplacements should be corrected, they were omitted. Duplicates of occurrences on the same locality were not removed at this stage, as they usually represented multiple occurrences that were found in close proximity to each other. Serious effort has been made to manually remove duplicates of the same specimen represented by accessions from multiple herbaria.

In ArcGIS Pro, a spatial join was performed to assign each specimen to a country, biome type, biome or anthrome. Polygon layers were matched to the specimens using spatial-join analyses, and the raster layer using an extract-values-to-points analysis. Specimens that had no data assigned because they were adjacent to the polygon or raster had their features manually matched to the closest feature. For all analyses the WGS 1984 coordinates system was used.

2.5 | IUCN Red List assessments

Data on the IUCN Red List status of Annonaceae were downloaded from the IUCN Red List website (www.iucnredlist.org) when published or were obtained as draft from the Global Tree Assessment (GTA) project. The draft assessments from the GTA project only contain Annonaceae species with a tree habit, not lianas. See Verspagen and Erkens (2022) elsewhere in this Special Issue for a discussion on the methodology used for the assessments made in the context of the GTA project.

3 | RESULTS

3.1 | Annonaceae distribution over biome types and biomes

Plotting all 67,966 specimens collated in this study on the world map shows that Annonaceae are distributed over almost every tropical, terrestrial longitudinal degree, but that they are restricted in terms of latitude (Figures 1, S1 and S2). Only in North America, the genus *Asimina* is completely distributed outside of the tropical realm. Central and South America contain more than half (61%) of the number of specimens analysed (Table 2). Together with Africa (27%), these two regions contain more than 85% of the specimens available for this study. Annonaceae are distributed across 109 of the 195 existing countries (Figure 2; Table S2). Only one genus is present on all continents on which Annonaceae are distributed: *Xylopia* (Table S3). In contrast, 78 genera out of a total of 108 have their specimens located on only one continent. The countries containing the most specimens (full list in Table S2) are Brazil (19,758), Peru (3708), Gabon (3304) and the United States (3256). Regarding the distribution of the specimens per genus across countries (Table S3), it appears that only 19 genera have specimens distributed in only one country, mostly due to small sample size.

Annonaceae are present in four of the six major terrestrial biome types (Table 3): the desert biome type, the grassland biome type, the temperate vegetation with trees biome type and the tropical vegetation with trees biome type. The desert biome type contains the least specimens (0.21% of the total specimens studied; Figure 3), although twice as many genera occur in that biome type in comparison to the temperate vegetation with trees biome type (Table 3). All genera are present in the tropical vegetation with trees biome type. This biome type contains approximately 95% of the specimens in this study (Tables 3 and S4); 65% of the genera found in this biome type are also restricted to it (Table S4). All the others are present in at least one other biome type, although generally for those genera, only very few specimens are found in those biomes. *Asimina* is a genus with a mainly temperate distribution. Two genera have collections from all four biome types: *Annona* and *Mitrephora* (Table S4).

Annonaceae specimens are present in 12 of the 14 analysed biomes. The Tropical and subtropical moist broadleaf forests contain both the most specimens and genera (68.5% of specimens, 46,512 specimens and 106 genera out of 108 genera; Tables 3 and S4). The Tropical and subtropical grasslands, savannas and shrublands rank second (18.8% of specimens, 12,796 specimens and 65 out of 108 genera; Tables 3 and S4). Only two genera are not included in the tropical and subtropical moist broadleaf forests: *Asimina* due to its temperate distribution and *Mwasumbia* as it is only present in the Tropical and subtropical grassland savannas and shrublands biome (Table S3). The biomes Deserts and xeric shrubland and Mangroves are separately shown in Figures 3 and 4

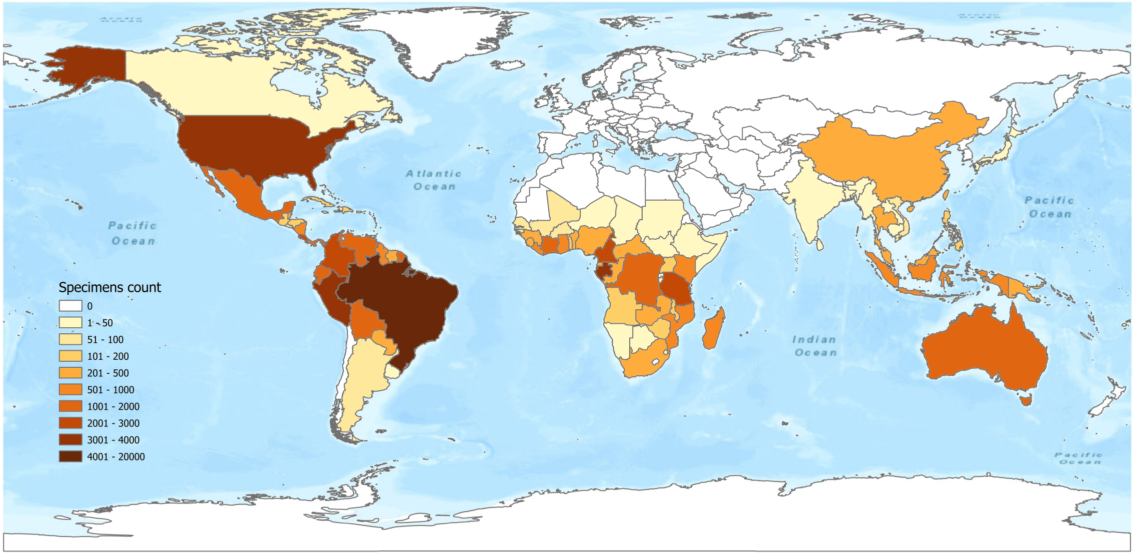

FIGURE 2 Number of specimens used in this study per country. The exact counts per country can be found in Table S2.

TABLE 3 Number of Annonaceae genera, species and specimens per biome type and biome based on our data set (taiga and tundra are not included in the generic biome types and biomes list since they did not contain any specimens). Names of the four generic biome types containing Annonaceae specimens are indicated in italics. The sum of genera of individual biomes per biome type can be larger than the number mentioned per biome type because of shared genera between biomes.

	Number of genera	Number of species	Number of specimens	Percentage of specimens
Desert biome type	16	41	142	0.2%
1. Desert and xeric shrublands	16	41	142	0.2%
Grassland biome type	29	84	351	0.6%
1. Flooded grasslands and savannas	20	51	243	0.4%
2. Montane grasslands and shrublands	19	45	108	0.2%
Temperate vegetation with trees (forests, savannas and shrublands) biome type	8	18	3291	4.8%
1. Mediterranean forests, woodlands, and scrub	1	1	1	<0.01%
2. Temperate broadleaf and mixed forests	5	8	1662	2.4%
3. Temperate conifer forests	3	4	98	0.1%
4. Temperate grasslands, savannas and shrublands	2	11	1530	2.3%
Tropical vegetation with trees (forests, savannas and shrublands) biome type	108	1,430	64,182	94.4%
1. Mangroves	52	249	1042	1.5%
2. Tropical and subtropical coniferous forests	17	65	477	0.7%
3. Tropical and subtropical dry broadleaf forests	48	303	3355	4.9%
4. Tropical and subtropical grasslands, savannas and shrublands	65	415	12,796	18.8%
5. Tropical and subtropical moist broadleaf forests	106	1351	46,512	68.5%

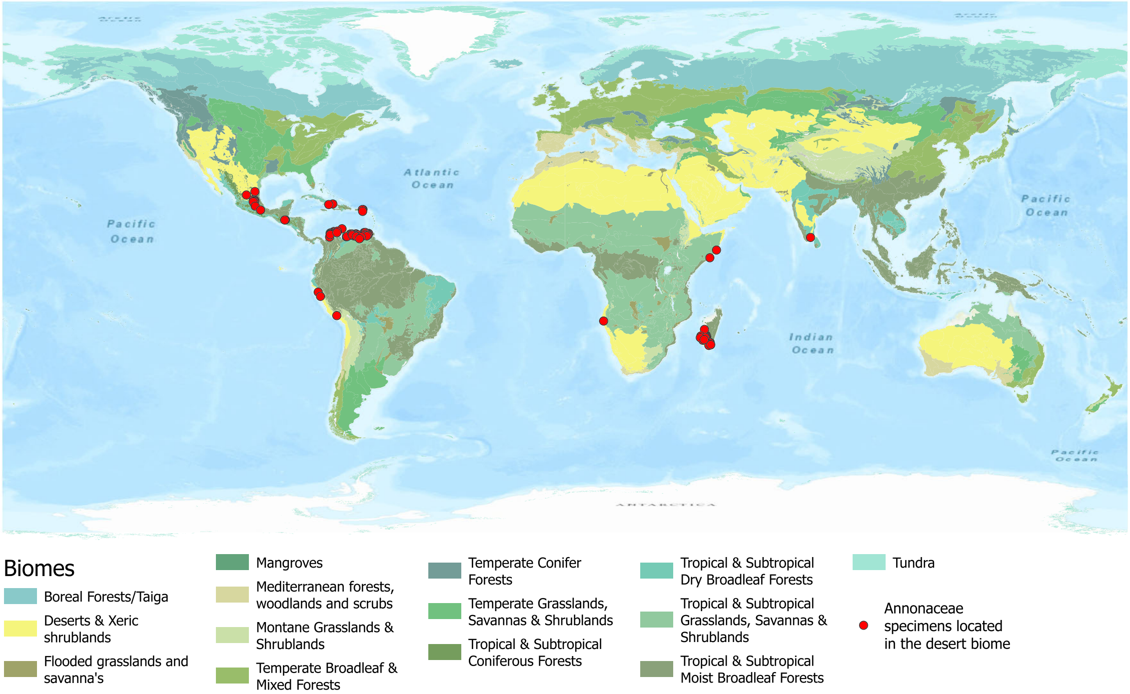

FIGURE 3 Distribution of specimens from Annonaceae genera found in the deserts and xeric shrublands biome. A single dot indicates a geolocated Annonaceae specimen of *Ambavia*, *Anaxagorea*, *Annona*, *Artabotrys*, *Fenerivia*, *Guatteria*, *Hexalobus*, *Huberantha*, *Mitrephora*, *Mosannona*, *Oxandra*, *Popowia*, *Sapranthus*, *Unonopsis*, *Uvaria* or *Xylopia*. More detailed maps per genus can be found in Figure S3.

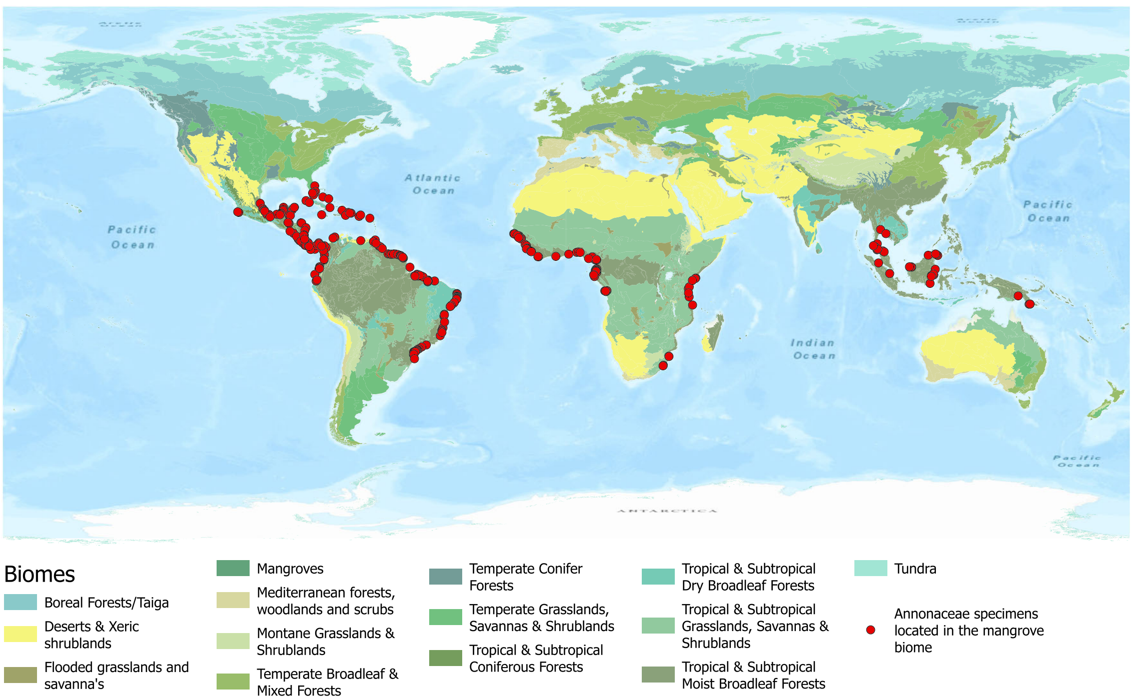

FIGURE 4 Distribution of specimens from Annonaceae genera found in the mangrove biome. A single dot indicates a geolocated Annonaceae specimen of *Alphonsea*, *Anaxagorea*, *Annickia*, *Annona*, *Anonidium*, *Artabotrys*, *Asimina*, *Bocagea*, *Cananga*, *Cleistopholis*, *Cyathocalyx*, *Cymbopetalum*, *Desmopsis*, *Desmos*, *Duguetia*, *Ephedranthus*, *Goniothalamus*, *Greenwayodendron*, *Guatteria*, *Hexalobus*, *Hornschuchia*, *Isolona*, *Klarobelia*, *Meiocarpidium*, *Melodorum*, *Mezzettia*, *Mitrella*, *Monanthotaxis*, *Monocarpia*, *Monodora*, *Mosannona*, *Neostenanthera*, *Orophea*, *Oxandra*, *Phaeanthus*, *Piptostigma*, *Polyalthia*, *Popowia*, *Pseudartabotrys*, *Pseudoxandra*, *Pseuduvaria*, *Pyramidanthe*, *Sapranthus*, *Sphaerocoryne*, *Toussaintia*, *Trivalvaria*, *Unonopsis*, *Uvaria*, *Uvariastrum*, *Uvariodendron*, *Uvariopsis* or *Xylopia*. More detailed maps per genus can be found in Figure S4.

TABLE 4 Number of Annonaceae genera, species and specimens per anthrome. Anthrome classification after Ellis et al. (2010) (see their Table 1 for a description of anthrome classes)

Name of anthrome	Number of genera	Number of species	Number of specimens	Percentage of specimens
Dense settlements				
Urban	63	356	1961	2.9%
Mixed settlements	59	364	1665	2.4%
Villages				
Rice villages	30	91	191	0.3%
Irrigated villages	27	57	173	0.3%
Rainfed villages	65	357	2707	4.0%
Pastoral villages	48	300	1909	2.8%
Cropland				
Residential irrigated cropland	26	90	209	0.3%
Residential rainfed cropland	86	615	6613	9.7%
Populated rainfed croplands	82	424	2630	3.9%
Remote croplands	49	160	409	0.6%
Rangeland				
Residential rangelands	72	590	8066	11.9%
Populated rangelands	66	587	7943	11.7%
Remote rangelands	65	388	3907	5.7%
Seminatural lands				
Residential woodlands	91	845	6945	10.2%
Populated woodlands	97	945	10,071	14.8%
Remote woodlands	87	587	6479	9.5%
Inhabited treeless and barren lands	37	142	484	0.7%
Wildlands				
Wild woodlands	76	502	5589	8.2%
Wild treeless and barren lands	7	10	13	<0.1%
Not assigned	1	1	2	<0.01%

because Annonaceae are not in general thought to be associated with these habitat types. There is one specimen of the genus *Monanthotaxis* found in the Mediterranean forests, woodlands and scrub biome on the most southern tip of South Africa.

3.2 | Annonaceae distribution over anthromes

Annonaceae are present in all of the 19 anthromes described by Ellis et al. (2010); Table 4). Several anthromes each contain around 10% of the specimens (Table 4): residential rainfed cropland (9.7%), residential rangelands (11.9%), populated rangelands (11.7%), residential woodlands (10.2%), remote woodlands (9.5%) and wild woodlands (8.2%). The populated woodlands anthrome contains the most specimens (14.8%) as well as the most genera (97; Table 4). The anthromes that can be seen as least disturbed by humans ('natural') together hold 17.7% of the specimens (remote woodlands 9.5% and wild woodlands 8.2%; Figure 5). Together, the before mentioned anthromes hold approximately 75% of the specimens (Table S5). Only two specimens from *Annona* could not be assigned to one of these anthromes. *Anaxagorea* and *Annona* were the only two genera with specimens assigned to all of these anthromes.

3.3 | Red List assessments

In total, data on 1225 species from 88 genera of Annonaceae were collated (Table 5). Nearly 50% of species did not meet the minimum requirements for assessment and were found to be Data Deficient (Table 5), in particular for South East Asian species (approximately 85%).

4 | DISCUSSION

4.1 | Natural distribution of Annonaceae

This study investigated the complete distribution of Annonaceae over generic biome types, biomes and anthromes based on a large data set of herbarium specimen data. The use of such data is increasingly

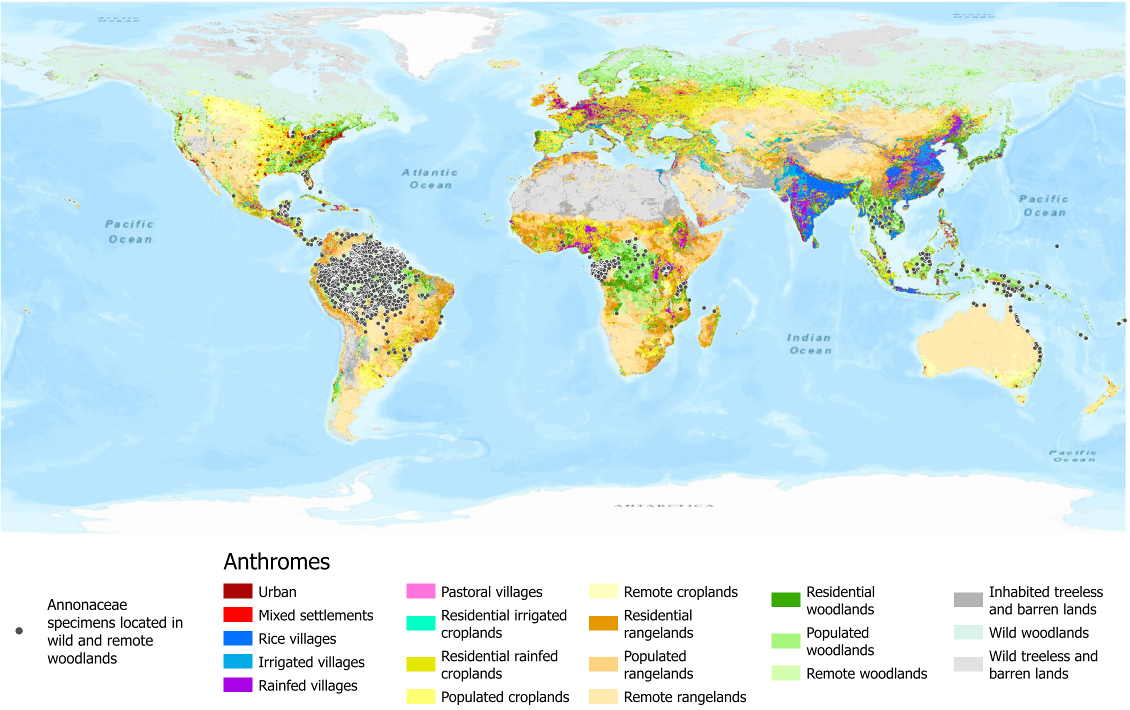

FIGURE 5 Distribution of specimens located in anthrome categories 'remote woodlands' and 'wild woodlands'. See Ellis et al. (2010) for a description of the anthromes depicted in this figure.

TABLE 5 Count and percentage per threat category for Red List assessments of Annonaceae species per continent

	CR[a]	EN[a]	VU[a]	NT	LC	DD	NE	Grand total
Africa-Madagascar	1	15	11	5	51	7	31	122
Asia		14	25	11	12	401		463
Neotropics	7	71	91	33	246	185		633
North America		1	1		4	1		7
Grand total	8	101	128	49	313	595	31	1225
Grand total (percentage)	0.7%	8.2%	10.4%	4.0%	25.6%	48.6%	2.5%	100%

Abbreviations: CR, Critically Endangered; DD, Data Deficient; EN, Endangered; LC, Least Concern; NE, Not Evaluated; NT, Near Threatened; VU, Vulnerable.
[a]Indicates 'threatened categories' according to the IUCN Red List guidelines.

popular and opens up new avenues for research (Dauby et al., 2016; Maitner et al., 2018; Maldonado et al., 2015). The total worldwide distribution across 109 countries recovered in this study (Figure 1) matches what is known from literature about the occurrence of Annonaceae. The results also confirm that Annonaceae predominantly occur in the tropical vegetation with trees biome type and associated biomes (Table 3), meaning that their distribution is concentrated around the equator (Feeley & Stroud, 2018). This is in line with the statement that Annonaceae are a good proxy for the occurrence of tropical rain forests (Punyasena et al., 2008).

Next to a tropical distribution, the data also show the occurrence of Annonaceae in dryer and lower temperature conditions. Nearly 5% of the specimens were collected in the temperate vegetation with trees biome type (temperate forests, savannas and shrublands). Of these, the large majority are from the mainly subtropical genus *Asimina* (Li et al., 2017). This genus is very well collected in the United States (mainly in Georgia and Florida states) with one species (*Asimina triloba*) naturally extending far into the temperate zone (including the southern part of Ontario, Canada; van Heusden, 1992; Table S2). It must be noted, however, that part of the 3235 specimens (Figure 1) included in this study will be of cultivated origin, because *A. triloba* (also known as the 'poor man's banana') is widely planted (Layne, 1996). Of the remaining collections from the United States, 90% belong to *Annona glabra*, which is also known from this country (Kral, 1960). Also in Africa and Madagascar, Asia, Australia and Argentina occasionally genera occur in the temperate vegetation with trees biome, such as *Fissistigma*, *Meiogyne*, *Melodorum*, *Mitrephora*, *Monanthotaxis* and *Trivalvaria* (Table S4).

A small fraction of the specimens (142 in total) were collected in the desert biome type (Table 3; Figure 3), including specimens collected along the pacific coast of Peru, Ecuador, Colombia and the Northern parts of Venezuela, Guatemala, Mexico, Cuba, the Virgin Islands, Namibia and South Madagascar and in Somalia and India. Whereas tropical regions are typically characterised by high annual precipitation, desert-like environments typically have extremely low rainfall (Woodward et al., 2004) and tend to experience high temperature variations due to their lack of vegetation (Guo et al., 2020). This biome is not regularly associated with Annonaceae. However, this biome includes xeric habitats, and 16 genera of Annonaceae have data points in such dry conditions (Tables 3 and S4). For the large majority of the genera, the proportion of the specimens assigned to this biome is around 0.6%, with a few between 1 and 4% (*Artabotrys* and *Popowia*: 1% and *Fenerivia*: 3.5%). We cannot assess if this low percentage is due to georeferencing errors or GIS projection issues (see below). However, the *Annona* specimens represent more than half of the total specimens located in the desert biome including xeric shrublands. One possibility is that this is due to the large number of cultivated specimens. On the other hand, Gottsberger (1999) postulated that *Annona* evolved and diversified in the forests of the Amazon Basin and adjacent areas but that the Central Brazilian Cerrados and the West Indies represent secondary centres of diversification (also based on Fries, 1931). He based his theory on the cytological studies that showed a development from diploid *Annona* species of humid, forested areas to tetra- or even hexaploid species of open, xeric vegetation types (Morawetz, 1984a, 1984b, 1986a, 1986b; Sauer & Ehrendorfer, 1984). Studies that model the distribution of *Annona* species (such as Rodriguez-Nunez et al., 2021) in an explicit phylogenetic context could provide more insight into the evolution of Annonaceae in drier habitats in the future.

Another unexpected find was that 1.5% of the specimens in this study were recovered in the mangroves biome (Table 3, Figure 4). These coastal wetlands are known for their halophytic plants. In Annonaceae, so far, no true halophytes are known. The specimens in this biome are mainly from species with larger distributional ranges. For instance, the genus *Guatteria* holds no halophytic plants (Maas et al., 2015), yet 18 *Guatteria* species (58 specimens) are reported from the mangrove biome (data not shown). Therefore, we expect that these species might have a wider ecological range than was expected for rain forest trees or that they grow within the mangrove biome in tropical-forest like conditions.

As expected, most Annonaceae specimens occur in the tropical vegetation with trees biome type around the world. Approximately 95% of collected specimens analysed here are from this biome type, although only approximately 70% are from the tropical and subtropical moist broadleaf forests biome (Table 3). This means that 30% occur in other biomes that have been researched far less, because the focus has mainly been on the tropical and subtropical moist broadleaf forests biome. Furthermore, much of the ongoing work on the family has focussed on the reconstruction of phylogenetic trees and morphological character mapping (e.g., Chaowasku et al., 2014; Couvreur et al., 2008; Photikwan et al., 2021; Su et al., 2008). The investigation of the ecological patterns in Annonaceae has received almost no attention, except for work on a few isolated groups (e.g., Couvreur, Porter-Morgan, et al., 2011; Li et al., 2017; Rodriguez-Nunez et al., 2021). However, the ecological patterns are highly relevant with respect to questions on for instance conservation and restoration ecology (Naveh, 1994), and biome shifting versus biome conservatism (Wiens & Graham, 2005). In case of the former, not only particular rare species or species with particular morphological traits might need conservation priority, but local ecological adaptations might be worthwhile to conserve too. In case of the latter, understanding if biome shifting or conservatism has been the more prevalent mode in the evolutionary history of Annonaceae helps in understanding which Annonaceae lineages will be able to transcend biomes more easily (or are more prone to extinction in their biome-confined distribution) in the face of climate change. Given that biome conservatism makes global climate change a danger to the world's flora (Wiens & Graham, 2005), we urge for the creation of high-quality data sets with species-level spatial data to gain insight in these processes, for Annonaceae specifically and for rain forest trees in general.

4.2 | Annonaceae in a changing world

Biologists still view the world through the lens of biomes, the most basic units to describe global patterns of ecosystem shape, process and biodiversity (Ellis & Ramankutty, 2008). However, for decades, human-dominated ecosystems already cover more of the terrestrial area than undisturbed ecosystems do (Mittermeier et al., 2003). For Annonaceae, it is clear that occurrences in truly 'wild' areas are only a minority (the remote woodlands and wild woodlands anthromes; Figure 5). These 'wild woodlands' areas coincide mostly with the well-known rain forest blocks: the Amazonian rain forest, the tropical rain forest of the Congo Basin and the tropical rain forest of South East Asia (including northern Australia; Brummitt et al., 2021). Approximately 70% of all Annonaceae genera (but only 8.2% of specimens) occur in this anthrome. The representation of Annonaceae as a 'tropical rain forest taxon' might give the impression of a group that mainly occurs in undisturbed areas, but that is not accurate (Table 4). When 'remote woodlands' (forest regions with minor land use without significant populations; Ellis et al., 2010) and 'populated woodlands' (forest regions with minor land use and significant populations; Ellis et al., 2010) are considered as well, at best approximately 32% of specimens of Annonaceae were collected in relatively undisturbed forests (Table 4).

This finding has important implications for understanding the ecology of Annonaceae as well as their conservation. It means that Annonaceae might occur in heterogeneous landscapes with clear human influences. Of course, we should consider the fact that a certain percentage of specimens were collected in potentially pristine forests or wild areas in the past. The size of the anthromes has substantially increased over the past 400 years (Ellis et al., 2010), and analysing the distributional data in an explicit temporal framework might yield more insight in this. In this way, the timing of collection could be linked to the habitat type at that time. However, in the absence of or with only little historical/archeological research across the tropical rain forest biomes (e.g., across the Congo Basin; Garcin et al., 2018), it might be very difficult to affirm that some areas were truly wild in the past although a temporal analysis of the specimen data might shed light on this. This also highlights another issue with a data set such as the one used here: Anthropogenic changes are relatively fast, and some of the data we use to understand the distributions of taxa might be from decades (or more) ago. Also, the anthromes data are already a decade old (Ellis et al., 2010). This introduces a bias in the results and would lead to an underestimation of the level of threat to such taxa. Although herbarium specimens are a common data source for determining the distribution of plant taxa (Nualart et al., 2017), this temporal bias is not often mentioned. For Annonaceae, this bias can well be true, as the experience of the authors is that Annonaceae are linked to generally little disturbed ecosystems. Based on this data set Annonaceae, only avoid human impacts in areas with the least potential for agriculture (such as tropical areas with low fertility soils). We have virtually no information on what this means, for instance, for the genetic structure of Annonaceae for which only a few studies exist (Collevatti et al., 2014; Helmstetter et al., 2020; Migliore et al., 2019; Piñeiro et al., 2021). Furthermore, Annonaceae only contain a few economically important species (e.g., some in the genus *Annona*; Larranaga & Hormaza, 2015 and *Cananga odorata* Benini et al., 2012), and therefore, their decline could easily go unnoticed (although locally they can be quite important and this impact might be felt much earlier). Another aspect that is worth further investigation is that our data set contains trees as well as lianescent species of Annonaceae. Lianas might respond very differently to the changing world, because it is known that lianas can for instance rapidly colonise abandoned agricultural fields that start to regenerate into forest (Schnitzer & Bongers, 2002; Selaya & Anten, 2008).

In short, it could be that Annonaceae occur without issues in heterogeneous human-influenced landscapes, but we cannot rule out that the species in the family might be actually threatened because of this. Therefore, we would need to know if taxa occurring more in disturbed areas are also more threatened.

4.3 | Threat assessments of Annonaceae

Next to spatial analyses, another way to assess the level of threat to a taxon is to look at the IUCN Red List threat assessments. For Annonaceae, 1225 species have published or draft assessments available (Table 5), most of these being trees. Approximately 20% of the assessed species fell in one of the three threat categories (Endangered, Vulnerable and Critically Endangered). This is about the same level as for plants in general (Brummitt et al., 2015). It seems therefore that Annonaceae do not stand out in terms of the currently assessed threat levels. However, the number of species assessed as Data Deficient represents just under half of the species assessed to date (Table 5). This difference is partly an artefact of data accessibility. It was noted before that although many organisations collect biodiversity data, these valuable data can often not be fully (re)used (Michener, 2015; Roche et al., 2015). Even when data are accessible on the internet (such as is the case for the Neotropics [BIEN] and Africa [RAINBIO]), these data might not adhere to FAIR principles, which means that they should be easy to find, combine or repurposed (Findable), Accessible, machine readable (Interoperable) and licenced for reuse (Reusable) (Reyserhove et al., 2020). Of course, the GBIF exists as an international infrastructure aimed at publishing open access, standardised biodiversity data. However, GBIF does not hold curated specimen information and is highly impacted by duplicates (Sosef et al., 2017) from the same specimen that are available across different herbaria. This can lead to inflated numbers of specimens in analyses. Although there are ways to clean these data (e.g., the CoordinateCleaner tool; Zizka et al., 2019), it is very difficult to know the level of certainty one can attach to the data. Furthermore, for the Asian draft assessments, mainly GBIF data were used that contained only few collections for many species. In combination with the fact that verifiable spatial data were often lacking, not enough specimens were available to make proper Red List assessments, leading to a Data Deficient status.

Digitising more specimen data and presenting them in a FAIR way also enables the mass assessment of threat levels of species for the IUCN Red List at, for example, continental levels (Stévart et al., 2019). For many of the assessments made in the context of the GTA project, assessment information on species was mass uploaded via the IUCN SISConnect portal. Although some depth is lost in the assessment with this method, it does not differ that much in terms of outcomes from the individual approach (Bachman et al., 2020; Dauby et al., 2017; Verspagen & Erkens, 2022). However, it is much faster. Therefore, in order to increase the speed at which Red List assessments are being made, the use of a standardised data format (Reyserhove et al., 2020; as for example proposed by Stévart et al., 2019) would be tremendously important. For using georeferenced specimen information, collectors should also start to record information such as the geographic and projected coordinates systems used. The settings of the GPS device ultimately affect both the data set and the layers used for the spatial analyses. Here, we found that in almost all cases, there was no indication regarding the different geographic coordinate systems used by the collectors of the specimens (or at least this data was not logged). Therefore, all data were treated here under WGS84. Unfortunately, this choice affects the positional accuracy of the individual data points and with that the level of accuracy of the analyses and Red List assessments. This issue deserves more attention in order to increase the quality of the distributional maps and the conclusion based upon them.

Our data set also underlines that there are large differences in numbers of (accessible) collections between the continents (Figure 2). Although one might first think this is a true reflection of the number of collected specimens or the result of collectors bias (ter Steege et al., 2011), for Annonaceae, it is also related to the accessibility of the specimens. For instance, ongoing research via the 'Herbonautes' citizen science project has digitised approximately 8000 Annonaceae specimens from Asia in the herbarium of the Muséum National d'Histoire Naturelle in Paris that were not yet included in this study (a non-negligible number are however duplicates; Couvreur *pers. comm*.).

Recently it was furthermore shown that especially small herbaria contribute unique occurrences of species that help to better understand the distributional ranges of these species (Marsico et al., 2020). This means that collaboration with local herbaria remains important also because much information on endemic species is present in those local herbaria (Brummitt et al., 2021). Unfortunately, these small herbaria are also often underrepresented in the online available data sets (Brummitt et al., 2021; Marsico et al., 2020). For the threat assessments, local specialists can also be involved in either drafting of assessments or the review step (as is being done via local IUCN Redlisting workshops already). This is an important quality check. At this moment in time, the draft assessments can be improved, and data that are not available in other ways can still be incorporated. Especially for species in the most remote and therefore least accessible regions, this information can make a large difference and change the Data Deficient assessment into one of the other categories. The Data Deficient category is therefore an important pointer for future research.

4.4 | Conclusion

In this study, we used the available spatial data on the pantropical plant family Annonaceae to study its distribution over biomes and anthromes. Although the general distribution of Annonaceae confirmed the well-established tropical rain forest distribution, less well known biomes were also identified as important and (deserts and xeric shrubland and mangroves) could be better investigated for future ecological research on Annonaceae. The anthrome analyses showed that less than one fifth of Annonaceae specimens were collected in areas that are considered truly 'wild' today. Data on published and drafted IUCN Redlist threat assessments for Annonaceae showed that the threat level at this moment in time is similar to that of other plant groups but that the high number of Data Deficient assessments points towards a large bias in data collection, especially for Asia.

In conclusion, in this UN Decade on Ecosystem Restoration, it is important to increase our understanding how different taxa are affected by the human induced, global changes in ecosystems. Especially for tropical forests, this is important given that more than half of all vascular plant species occur there. Our study shows that even for a taxonomically well-studied tropical plant group such as Annonaceae, we have little understanding about the larger scale distributional and ecological patterns, let alone the threats that individual species might face in the future. Because we believe that for most other plant groups the situation will be similar (or worse), we urge in general to invest in (1) the exploration of ecological requirements of species in relation to their genetic patterns, in order to understand the impact of ecosystem changes, (2) research on distributional patterns in a temporal framework as the available data collected over decades might not reflect current distributions over biomes and anthromes well and (3) high-quality spatial data collection that should adhere to the FAIR data principles, so that the quality of spatial analyses as well as IUCN Redlist assessments will increase.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

RHJE and LMPB conceived the idea for this study; LMPB, KR and AC collected and cleaned the data; RHJE and LMPB analysed the data; NV, AC and TC were involved in the analysis of the threat assessment; RHJE, LMPB and TC wrote the manuscript; RHJE and LMPB compiled the supplementary materials.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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